

ACTIVITY BUDGETS AND REPRODUCTIVE COSTS IN A GROUP OF FEMALE  
WEDGE-CAPPED CAPUCHIN MONKEYS (CEBUS OLIVACEUS)

BY

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By

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The relationship between reproductive state and activity budgets in female wedge-capped capuchin monkeys (Cebus olivaceus) was examined. The study tested the hypothesis that female capuchin monkeys meet the energetic demands of pregnancy by altering their activity schedules and that those alterations would show up as significant differences in foraging, feeding, moving, or resting time. It also tested whether reproducing females have a higher success rate when foraging and whether the presence of possible competitors in the near vicinity of a foraging female affects her success

The data showed no significant differences between the activities of reproductive and nonreproductive females.



It seems probable that during the dry season, the animals are losing weight and incurring an energy debt. During the wet season, capuchins are not food-limited; their caloric intake is often limited only by their digestive processes.

Reproductive females may gain less weight during the wet season than other females, due to the increased costs of supporting an infant. The observed two-year cycle among the study animals would enable reproductive animals to reproduce in one wet season, and spend the next one building up their reserves of fat, protein and other nutrients. Under these circumstances, their activity schedules would not be different from those of other females, and the data may reflect the real situation. This situation is partly due to adaptive traits that fit the animals to their habitat, and partly due to the unique conditions at the study site that make it unusually benign at present for the monkeys.

Reproductive females did not have a higher foraging success rate than nonreproductive females and the presence of other animals near a female did not appear to affect her foraging success rate.

## INTRODUCTION

Female nonhuman primates spend a great part of their reproductive lives either pregnant or lactating. Silk (in prep.), for instance, has estimated that female baboons (Papio cynocephalus), which give birth at approximately two-year intervals, are pregnant for nearly one quarter of their adult lives. Reproduction involves a considerable cost in energy, particularly for mammals, which as a class have a heavier and more extended parental commitment than any other vertebrate taxon. In primates, that parental commitment is unusually long compared to other mammals (Gould, 1977). Female mammals bear the bulk of the energetic costs (Vaughan, 1978; Eisenberg, 1981; Millar, 1981, 1977). This cost is incurred in several ways.

### Pregnancy

The energetic costs of pregnancy for an eutherian mammal include not only the metabolic expenditures of building an infant, but the added cost of carrying the weight of the fetus and associated tissues and fluids (Silk, in prep.; Silk, 1986; Leutenegger, 1973). and the demands of a higher resting metabolic rate (Blackburn and Calloway, 1976). Hytten (1980) has shown that overall caloric requirements in human females during pregnancy may be as much as 25% higher than

normal. Portman (1970) estimated the daily energy requirement for an adult female rhesus monkey at 100 Calories (=kilocalories) per kilogram of body weight and that for a gestating female at 125 Calories per kilogram. Portman also estimated that nonhuman female primates may require as much as 25% more protein during pregnancy and lactation, a figure that compares with Blackburn and Calloway's (1976) finding that pregnant women received about 17% of their energy from protein, compared to a pre-pregnancy rate of 11%-13%. Rioppelle and Hale (1975) demonstrated that gestation in Macaca mulatta varied by as much as nine days as a result of dietary protein. Kaminetzky and Baker (1980) have pointed out that pregnant women are less efficient in their utilization of protein, adding to the already increased demands of the pregnancy itself. Both energy and protein requirements increase greatly over the final months of pregnancy, when the fetus gains weight most rapidly (Silk, in prep.), although Kaminetsky and Baker have pointed out that the protein cost of pregnancy is somewhat evened out over the entire term by the storage of excess protein in maternal tissues during early pregnancy, and its transfer to the fetus at a later stage. Widdowson (1981) has observed that protein and energy are essentially inseparable, since it is almost unknown for an animal to gain protein without an associated gain in energy.

Blackburn and Calloway (1976) have documented the extent of energy expenditure in reproductive human females. They

note that normal activity level and the extent to which activity can be reduced are important factors in the energy budget of pregnant women. However, their study involved sedentary women; the energy budgets of other primates are not so amenable to alteration by reduction of activity. Frisch and McArthur (1974) have shown that the onset and maintenance of menstrual cycles are related to a minimum weight/height ratio representing a critical fat store. Frisch (1978) has also shown that undernutrition may increase interbirth intervals and the risk of miscarriage, and delay the onset of sexual maturity in humans. Mori (1979) found that a fall in birth rate in a Macaca fuscata population was associated with a fall in mean female body weight. Kaminetzky and Baker (1980) have pointed out the consequences of maternal malnutrition on human infants and emphasized the importance of trace elements in the maternal diet. Fetuses of malnourished mothers experience developmental problems and the evidence suggests that they may never reach full growth and development of neural tissue. The authors also note that "An insufficient weight gain during pregnancy increases the risk of low birth weight. . . Furthermore, the patient with inadequate caloric intake may have deficiencies of specific nutrients" (p.414). They list eight trace elements--iodine, cobalt, copper, zinc, chromium, selenium, magnesium and manganese--that are essential to mammals; lack of any of them can affect a pregnancy, and the proportions of these elements in the body vary with pregnancy and life stage. The

concentration of iron in the body is higher at birth, for instance, than at any other point in life.

### Lactation

Lactation is the most energy-demanding aspect of mammalian reproduction (Jolly, 1985; Barclay, 1989; Kunz, 1987; Altmann, 1980; Dunbar and Dunbar, 1988; Nicolson, 1986). Lee (1987) has suggested, in fact, that the primary influence of nutrition on fertility operates through the high energetic demands of lactation. Widdowson (1981) has shown that some females actually store fat during pregnancy for the later demands of lactation. Portman (1970) has estimated that energetic costs for lactating female rhesus monkeys rise from the 125 Calories per kilogram of body weight per day needed during pregnancy to 150 Calories/kg/day.

Davis and Bauman (1974) have summarized the metabolic aspects of lactation; they point out that the demands of lactation alter the general metabolism of a female mammal. The blood supply is redistributed, the general metabolic rate increases, and there is a dramatic increase in the demand for nutrients. Flatt and Moe (1974) have stated that although all nutrients are extremely important, a limited supply of energy is most frequently at fault in lower milk production among domestic animals. Touchberry (1974) noted that varying the composition of feed given to cattle had little effect on the

percentages of fat, protein, and non-fat solids in their milk. The effects of varying feed are seen in quantity, rather than quality of milk. Energy costs of lactation may vary among species, since the composition of milk varies (Ofstedal, 1980). Ofstedal has also pointed out that milk composition may vary individually at different stages of lactation. Randolph et al. (1977, cited in Eisenberg) have shown that in the rodent genus Sigmodon lactation may be twice as costly energetically as gestation. Deinhardt (1970) found that marmoset milk has five times the protein content of human milk, making it considerably more costly in energetic terms for marmosets to produce milk than for humans. Cost differences may also be related to length of lactation; Eisenberg (1981) has pointed out that larger mammals tend to lactate longer, but the energetic cost is less per day and they wean their young at smaller body sizes compared to adult body weights.

Millar (1977) has stated that late lactation is energetically the most critical period of the breeding cycle. This needs clarification. The energy demand on lactating females rises as the infant grows larger, until it peaks at the point where the infant begins to feed itself. At that point, the energy demand begins to drop, although lactation may continue for some time.

#### Transporting of Infants

In many mammalian species, females often carry their offspring. Carrying is required constantly at first, then for decreasing proportions of time as the infants become independent. This is true for most Old World primates (Roonwal and Mohnot, 1977) and about half of all New World primates (Wright, 1984; Napier and Napier, 1985; Kleiman, 1977). In the other New World primates, the male is assumed to be responsible for most of the infant carrying. Hoage (1983) found in Leontopithecus r. rosalia that infants are usually carried from birth to about 12 or 14 weeks of age. Infants generally remain with their mothers until about 14 days after birth before first being handed over to another family member, usually the father. Mothers are still the principal carriers through the third week of the infant's life, with fathers as secondary carriers. But in the fourth through twelfth weeks, the father is the principal carrier. However, Box (1977) has demonstrated that in captive Callithrix jacchus, the generally accepted idea that the adult male does the bulk of infant carrying may not be true. Box's data showed considerable variation both within and among family groups of marmosets, but gave little support to the assumption that males were the major carriers of infants.

Even relatively independent juvenile Cebus olivaceus may still require carrying when stressed or tired (pers. obs.). The energetic cost to primates of carrying infants is sufficient to be considered a major portion of parental investment (Altmann, 1980; Lancaster, 1971; Blaffer-Hrdy,

1976; Quiatt, 1979) and a possible factor in parent/offspring conflict (Trivers, 1972, 1974).

The energetic costs of transporting infants are incurred in two ways: the transporter must expend energy to do the carrying (Box, 1977; Nicolson, 1986; Wright, 1984) and must also suffer the effects of decreased foraging or feeding efficiency due to the encumbrance of the infant or infants (Altmann, 1980). Wright (1984) has shown that male Callicebus and Aotus have a significantly lower foraging efficiency when carrying infants.

Since transport commonly occurs synchronously with lactation, its energetic cost is difficult to estimate, although Wright has observed that among primates the costs are proportionately greater in smaller species. Whitten (1982) has estimated that carrying an infant can add as much as 17 percent to the energy costs of movement for a male vervet. The fact that transport is the major category of allomaternal care among many species (Jolly, 1985; Blaffer-Hrdy, 1976; Lancaster, 1971; McKenna, 1979; pers. obs.) is probably significant, but see Quiatt (1979).

#### Other Care-giving

Infants require other forms of care-giving, as well. These include protection, play, grooming, defense and keeping warm, for instance (Trivers, 1972; Gray, 1985;). Relative costs for these activities are extremely difficult to estimate, but undoubtedly exist. Wright (1984) has shown that



male Callicebus spend a significant amount of time playing with their infants, but in species where other infants are available for play, this may be less important. Protection of infants can also require energy, especially in species such as Callicebus, that have high infant losses to predators. Infant defense may also expose the care-giver to increased personal danger, as Wright has observed.

Food transfer may be an important aspect of caregiving in some species, with an attendant cost in energy to the caregiver. Hoage (1983) has shown that young lion tamarins (Leontopithecus r. rosalia) in captivity still have a 50% success rate at acquiring food from other animals during the 29th to 40th weeks of their lives; even after that, when their success rate drops, they continue to get food from other animals by stealing. Whether these figures would be as high under more natural conditions is difficult to estimate.

#### Extended Care

Clarke and Glander (1984) have pointed out that in many primates, parental care does not stop with the end of lactation. Rather, as the infant acclimatizes to its physical and social environment, it continues to learn through interaction with the parent. This process might be expected to be more extended in the case of female infants of species in which young males emigrate. In such systems, female infants must adapt to a social structure in which they will presumably spend their entire lives. Their positions within

those systems will depend in large part on the positions of their mothers. Johnson (1986) has suggested that female red-necked wallabies incur further significant costs through increased tolerance of competition from their offspring and that such costs represent a form of prolonged maternal investment.

#### Female Energy Demands

Female primates, then, like other mammals, are faced with increased energy demands if they are to reproduce. Millar (1975) has stated that, among mammals, "Females do not appear to accumulate much energy prior to breeding, but support their offspring primarily through increased feeding when demands are greatest." However, a number of studies have documented the link between pregnancy (Frisch, 1978; Frisch and MacArthur, 1974; Kaminetzky and Baker, 1980) or reproductive success (Wauters and Dhondt, 1989; Chapman et al., 1990) and initial fat or protein levels in females. But the nutritional reserves necessary to initiate reproduction are not sufficient to carry a female through both gestation and lactation.

If females are not able to stockpile significant energy reserves to carry them through the reproductive process, it might be expected that they would meet the added demands

through behavioral adaptation. They could do this in two ways.

First, they could increase or alter their nutritional intake. Females could do this by becoming more efficient foragers (evidenced by a higher success rate when foraging) or by increasing the rate at which they feed, but they are more likely simply to spend more of their time feeding, as Millar has suggested. Dunbar and Dunbar (1988) state that "...the energy cost to the female must increase with time, and this should be reflected in a steady increase in the amount of time she spends feeding throughout the period of lactation," (p.970).

In her study of baboons (Papio cynocephalus), Silk (in prep.) found that "Females who produced surviving infants spent progressively more time feeding as their pregnancies progressed..." (p.23). Gautier-Hion (1980) found that female Cercopithecus monkeys alter their food choice to increase protein intake during pregnancy and lactation. Altmann (1980), in her model of maternal time budgets for Papio cynocephalus, predicts that a female's feeding time requirements will be approximately a linear function of her infant's age. Her model makes the assumption that only social time is available for use as extra feeding time, but Dunbar and Dunbar (1988) point out that other baboon studies have shown that resting time, rather than social time, acts as a reservoir that can be utilized for additional feeding. Dunbar and Dunbar tested Altmann's model in their study of

Theropithecus gelada. They found that geladas gave up all resting time and part of their social time during the peak of lactational energy drain in order to increase feeding time.

Second, they could decrease general or specific activity levels, and thus expend less energy. It is somewhat doubtful how effective a drop in overall activity might be except in the presence of a superabundance of food, since the loss in food intake might offset the energy gain from resting. If animals are conserving energy, the logical activities to curtail would be social ones, since they do not contribute as strongly to the energy balance. Terborgh (1983) has suggested that large, omnivorous primates such as Cebus have comparatively little time for social behavior because of the strictures of their feeding habits. However, both Robinson (1986) and O'Brien (1990), working with the same population of monkeys as this study, present data to the contrary. If the females are in fact conserving energy, then a decrease in general or specific activity levels should show up as an increase in time spent resting.

If female primates are to meet the added energy demands of reproduction behaviorally, then, their options are to increase their food intake, reduce their energy output, or both of the above. Those adaptations should show up as differences in their activity budgets. This study was designed to test that premise by examining the time budgets of female capuchin monkeys (Cebus olivaceus).

Cebus olivaceus

Cebids are generalized omnivores (Eisenberg, 1989; Terborgh, 1983; Freese, 1983) that make use of every level of their forest habitat, from the ground to the canopy. They are extremely intelligent and appear almost tireless as they go about their daily routines. They are quadrupedal, and Napier and Napier (1985) describe them as climbers, springers and branch runners. Individual capuchins can be easily distinguished in the field by a combination of characteristics, such as facial markings, pelage, size, age, sex and behavior (Robinson, 1981; Izawa, 1979; Oppenheimer, 1973).

Cebus olivaceus, the wedge-capped or weeper capuchin, is a medium-sized monkey, with a head-plus-body length of approximately 45cm and a tail of the same length. Its dentition is typical of the Cebidae, with 36 teeth (2/2-1/1-3/3-3/3 x 2) (Napier and Napier, 1985), the canines being prominent. Typical body weight for a female is 2.3 kg (Eisenberg, 1989), with males almost a kilogram heavier. Its distribution is "in northern South America from northwestern Venezuela across through the Guyanas south to the Amazon" (Eisenberg, 1989, p.251). Capuchins are capable of living to at least thirty years of age; females can first give birth at six years of age, although they may not do so (Robinson, 1988a). Females reproduce on the average every two years. Peak birth months for the study group in Venezuela are June and July.

Males, on the other hand, are not considered adult until approximately 12 years of age, when they attain full size and adult pelage. Capuchins are found typically in single- or multi-male groups ranging in size from a few to as many as 35 or 40 animals. Typically, a group will contain a dominant adult male and one or more subadult males, along with a number of females and their offspring. Females align themselves in matriline, which determine social position. Young males typically emigrate from their home groups.

Robinson and Janson (1986) have described Cebus olivaceus as a "ripe fruit specialist." This is quite accurate but tends to obscure the species' reliance on two other food sources. The first of these is invertebrates. Terborgh (1983) has described Cebus as "searchers" rather than "pursuers" of invertebrates; Robinson and Janson (1986) refer to them as manipulative foragers. They actively seek out insects, snails, and other invertebrate prey by probing, investigating or tearing apart any likely spot. They can be highly destructive, breaking branches and tearing off bark to search for wood-boring insects or grubs. Izawa (1979) has provided a detailed description of the feeding behavior of the closely related black-capped capuchin, Cebus apella. Invertebrates are the major protein source for cebids, and thus have an importance beyond their caloric content. They are sought throughout the year, but they seem to be more abundant in the wet season. At that time, major invertebrate

events such as caterpillar "flushes" and carpenter ant migrations provide the monkeys with an abundance of prey.

The monkeys' other major food source is the palm, Copernicia tectorum, found throughout their home range. Capuchins utilize the palm in a similar fashion to that described by Terborgh for Cebus apella, making use of every edible part and even being able to extract the pith from the tough, woody petioles of the palm fronds. The pith is a dry-season staple of the capuchins on the study site. Terborgh's description of palms as the "primary ecological refuge" for C. apella is also applicable to C. olivaceus.

Capuchins are basically ripe fruit specialists, however. Robinson (1986) has definitively described their foraging and feeding patterns, listing the different fruits available throughout the yearly cycle. In the dry season, the monkeys typically visit a permanent water source at some time during the day. Individual animals typically rest for short periods during the heat of the day, within the framework of the group's foraging movements.

The bulk of present knowledge of Cebus olivaceus comes from a series of investigations of the animals that are the subjects of this study. This population of monkeys has been studied over a period of more than 15 years. Oppenheimer and Oppenheimer (1973) conducted a brief study of one group of Cebus olivaceus in the study area; they described social behavior, visual displays and vocalizations. Robinson (1988a, 1988b, 1986, 1985, 1981) has made an extended study of the

Cebus population in the study area, particularly the group described here.

A 1981 paper by Robinson found that the study animals arranged themselves in consistent, predictable configurations while foraging. The most advantageous position in the group, center front, was typically occupied by the dominant male and female, along with other animals tolerated by the dominant female. Other animals were arranged predictably according to their age-sex classes, and these positions were important in terms of foraging requirements and predation risks.

Robinson (1984) examined the pronounced diurnal variation in Cebus foraging. The study animals exhibited a pronounced foraging pattern in the dry season, but none in the wet. At all seasons the animals tended to feed on ripe fruit early in the morning. He also looked at the relative importance of environmental versus internal constraints on foraging patterns.

Robinson's 1986 paper examined the relationship between the group's foraging behavior and the distribution of resources, looking at the way in which behavioral mechanisms regulated group foraging. Monkeys were less selective in seasonal periods of food scarcity. The amount of time they foraged increased with resource abundance, but only in the dry season, when food was scarce. During the wet season, when resources were plentiful, foraging time was determined by the digestive capacities of the animals. Patterns of movement and use of space by the group were predictable from the specific



distribution of the most common resource in each month. Robinson concluded that the foraging monkeys possessed considerable information on resource availability and abundance within their range, and that they based their movements on that knowledge. Large groups could more easily defend fruiting trees, and larger ranges were advantageous in ensuring that fruiting trees were available throughout the year.

In his 1988a paper, Robinson looked at reproductive success as a function of group size and found that female reproductive success, expressed as higher age-specific fecundity, was much higher in large groups. Apparently this was a result of large groups' ability to monopolize fruit trees. Large groups were able to displace smaller groups during intergroup encounters, driving them from trees containing ripe fruit. The single breeding male in a large group had a longer breeding tenure, higher reproductive success and access to more females with higher reproductivity than his counterparts in smaller groups. Group rank in relation to other groups was determined by the number of males in each group; Robinson attributed the higher number of resident males in larger groups to their longer average time with the group. That longer residence time he explained as a result of the higher average reproductive success of breeding males in larger groups.

Robinson's 1988b paper suggested that group structure of the study animals resulted from demographic parameters,

rather than intragroup social interactions. Non-adults made up an average 60% of a group, the percentage increasing with group size. Higher female survivorship, a biased birth ratio, and sexual bimaturism resulted in a strong female-biased sex ratio among adults.

Fragaszy (1986) found pronounced sex differences in time budgets and foraging behavior of the study population. Adult females exploited a greater variety of plant substrates, obtained more protein from plant sources, and/or a greater diversity of nutrients than adult males. Fragaszy attributed these differences to the females' higher metabolic rates, associated with the needs of growth and lactation.

De Ruiter (1986) confirmed that time budgets were a function of group size, and suggested that the explanation lay in an adjustment to predation risk and intra-group food competition. Members of small groups scanned more and foraged at higher elevations within the forest than members of large groups. Intra-group food competition in the large group affected diet, travel distances and social behavior.

Srikosamatara (1987) confirmed that intragroup feeding competition was more evident in large groups than in small ones, and that members of large groups used more vertical strata in foraging, interacted more, spent less time feeding on fruit resources, and showed movement patterns different from those of small group members. Some intragroup competition in both large and small groups was alleviated by a shift from clumped resources (fruit) to more evenly

distributed ones (insects) in times of scarcity.

Srikosamatara also confirmed that members of large groups scanned less and spent more time on the ground, and that they were able to displace smaller groups and thus monopolize clumped food resources.

O'Brien (1990) compared patterns of social behavior between different classes of females and determined the importance of group membership and individual differences among females. His detailed study showed that females in small groups minimized their interactions with other group members and that their rank, relatedness and avoidance of aggression by withdrawal from the group all affected female-female interactions. In addition, reciprocal grooming was concentrated among high ranking and adult females. High ranking females were aggressive against lower ranking females, with supplantations (but not fights) limited primarily to foraging periods. They groomed high-ranking males, and were aggressive toward low-ranking ones. Several factors affected allomaternal behavior, including female rank, age and relatedness to the infant. O'Brien attributed the increased dominant, affiliative and cooperative behavior in large groups to tension resulting from increased intragroup competition. In general, females direct affiliative and cooperative behavior toward group members that are related or high ranking. They are aggressive toward lower ranking, peripheral females and subadult males.

Norris (1990) analyzed the semantics of Cebus alarm calls. He used recordings taken in the field, experiments with released snakes, and playback experiments to demonstrate that capuchins used alarm calls to identify threats as well as to give information such as the location of the threat.

### Hypothesis

As a result of the above studies, a considerable amount is known about population demography, reproduction, social structure, foraging behavior and predation avoidance in Cebus olivaceus. This study was designed to fill a remaining gap in our knowledge of their ecology by looking at the relationship between time budgets and reproductive status among females. The study was designed to test the hypothesis that female capuchin monkeys (Cebus olivaceus) meet the energetic demands of pregnancy by altering their activity schedules and that those alterations would show up as increases in foraging, feeding or resting time. It was also designed to determine whether reproducing females have a higher success rate when foraging and whether the presence of possible competitors in the near vicinity of a foraging female affects her success rate.

## METHODS

### Study Site

The study site was centered on a ranch, Fundo Pecuario Masaguaral, in the llanos of central Venezuela, approximately 50 kilometers south of Calabozo, in Guarico state. At an elevation of approximately 100m above sea level, the ranch has been maintained as a wildlife refuge since 1944. Vegetation on the ranch has been described by Troth (1979) and Wiley and Wiley (1980). Although it lacks many of the vertebrate species presumed to have occurred there originally, much of the habitat remains relatively unchanged, particularly in the gallery forests along two rivers, the Rio Guarico and the Cano Caracol, at the eastern end of the ranch.

This gallery forest is the home of at least 11 groups of capuchin monkeys (Robinson, 1986). It is a partly deciduous forest, heavily interspersed with palms (Copernicia tectorum), and with a well developed understory. Trees rarely exceed 20 m in height. On the study site the forest is about 4-5 km wide, grading into shrub woodland and then grassland as distance from the river increases. Most of the year's rainfall (average 1,450 mm) occurs from May to October.

During the wet season the forest floods, and standing water may remain in some parts into December.

The study area is crisscrossed by a gridwork of trails at 100m intervals, running north/south and east/west, and extending over the properties of three cattle ranches (Masaguaral, Hato Flores Moradas and Finca Torres). The trails originally were constructed by Robinson and have been maintained by subsequent researchers. Although locational data were not part of the study, the marked trails were often useful for orientation and location of specific sites, such as fruiting trees or sleeping trees. Since data were obtained by following individual animals at close range, the trails were generally used only serendipidously during data collection.

#### Study Group

All animals sampled were originally part of one group, hereafter referred to as Main Group. Main Group's original size varied from 35 to a high of 42. However, in December of 1984, a subgroup of nine individuals (two low-ranking males, two low-ranking females and their female offspring, and the male infant of one of the females) split off from Main Group and established itself as a new, independent group. Three of the sample animals were among those that left, including the two females with surviving young. This new group, hereafter referred to as Splinter Group, could not be located for a

period of three months following the split, and this resulted in a gap in the data for those three animals.

The monkeys of Main Group were originally habituated to the presence of observers by Robinson and were subsequently studied by the researchers mentioned previously. Tolerance varied among individuals, but many of the monkeys could be approached to within two or three meters. Despite this habituation, some animals were initially uneasy when they realized they were being individually followed for long periods of time. Previous observers had not conducted focal-animal samples of this length. Sample animals soon adjusted, however, and became generally indifferent to the persistent presence of an observer.

Individual capuchins are distinguishable by a variety of physical characteristics, the most notable of which are their facial markings (Oppenheimer, 1973; Izawa, 1979; Robinson, 1981). With practice, it is possible to distinguish all members of even a large group such as Main Group, which contained 37 individuals before it fissioned in December. Eight females of Main Group were selected for sampling; a ninth was added in July, 1984, when she appeared with an infant.

#### Sampling

Sampling began in May, 1984, and continued through May, 1985, for a total of thirteen months. The basic sampling unit

was a forty minute focal-animal sample (Altmann, 1974) during which time one monkey, the focal animal, was followed and all its activities recorded, along with their start and stop times. During that period the animal's activity was classified into nine categories, called states. According to Altmann (1974), a state is any behavior that has an appreciable duration in time and states are distinguished from events, those behaviors that lack duration. Of course, as Altmann points out, any behavior must have some duration; for the purposes of this study, events were identified as activities that were by their nature usually of very short duration and occurred within the context of one of the defined states. For instance, an animal might give a particular type of call (event) while moving (state) or momentarily interrupt its feeding to give an aggressive lunge toward another animal that had approached too closely. States were categorized as one of the following:

- 1) foraging: actively seeking invertebrates or small vertebrates;
- 2) feeding: eating fruit or other vegetable matter;
- 3) moving: directed movement not a part of foraging behavior;
- 4) lying;
- 5) drinking;
- 6) sitting;
- 7) grooming another animal;
- 8) being groomed by another animal;



9) other activities.

Each five minutes during the 40-minute sample, an instantaneous sample was taken (Altmann, 1974). During this instantaneous sample, the nearest neighbor to the sample animal was noted, along with its estimated distance ( $<1$ ,  $<2$ ,  $<3$ ,  $<5$ , or  $<10$  meters). If no monkey was observed within 10 meters, "none" was entered. Other details were also noted, such as whether the animal was foraging, and if so, its success or lack of success. If it was successful, the foraging object and substrate were noted.

Each animal was sampled three times during the morning and three times during the afternoon each monthly sampling period. An effort was made to spread each animal's samples out over the sample period. Sampling began at first light (between 6:00 and 6:30 a.m., depending on season) and continued until dark. The first animal encountered in the morning was sampled first; as soon as that sample was finished, another animal was sought, and so forth. If it was not possible to complete an entire forty-minute sample, the data were kept but an attempt was made to replace them with a complete sample. Whenever possible, samples were taken on consecutive days and in as few days as possible in order to minimize the effects of environmental variables.

Generally, sampling was completed in four or five days. On some occasions, however, it was impossible to keep the schedule. Individual animals or the group could not be

located or sampled, or samples were cut short and could not be duplicated. These were the exceptions, rather than the rule. However, as mentioned above, three of the nine sample animals were part of the Splinter Group, which could not be located for three months.

All data were recorded in the field using microcassette voice recorders, then transcribed onto data sheets. The data were transferred to disks using an Apple IIe computer and Appleworks software, then uploaded to the VAX system at the Institute of Food and Agricultural Sciences, University of Florida, for further sorting. Eventually the data were downloaded into MS Dos for analysis on PC-compatible machines at the Florida Cooperative Fish and Wildlife Research Unit, University of Florida.

### Analysis

Statistical analysis was performed using PC SAS (Schlotzhauer and Littell, 1987). The data were tested for normal distribution but normality could not be assumed, probably due to small sample sizes.

Data were sorted by month in order to minimize possible confounding effects of environmental variables. The percentage of the month's total sample time for each monkey that was allocated to each activity was determined. Sample animals were initially divided into two classes for comparison: those that reproduced in a given year versus

those that did not. For 1984, there were four nonreproductive and five reproductive animals. Two young were born in June and three in July.

The gestation period for Cebus olivaceus is approximately six months (Robinson, 1986). Total percentages for each group for each activity were compared for the months of May through December, 1984. Further classification of the animals into nonreproductives (4), reproductives who lost infants (3), and reproductives who kept their infants (2) reduced the sample sizes to a level that was too small for statistical testing, so both categories of reproductives were lumped for the months of July to December.

In 1985, an unusual situation developed, in that all six sample animals in Main Group produced infants. Since data for the months of January through March were only available for Main Group, no comparisons between reproductive and nonreproductive females were possible. It is worth noting that three of the reproductive animals in 1985 were those that lost infants in 1984.

Two statistical tests were applied to month-by-month comparisons of the two classes of females for 1984. The first was a Wilcoxon Rank Sum Test. It is a nonparametric analogue to the two-sample t-test. The measurements for both samples are pooled and ranked, then the ranks for each sample are totaled (McClave and Dietrich, 1982). Large differences in the rank sums indicate differences in the samples. The

Wilcoxon test's only assumption is that of independent observations (Schlotzhauer and Littell, 1987).

The second was a Spearman Rank-Order Correlation, which yields a value between -1 and +1. The Spearman test ranks the data, in this case by activity, and estimates the amount of correlation between the two sets of rankings, using the rank correlation coefficient,  $r_s$ . A perfect positive correlation would yield a value of +1, a perfect negative correlation a value of -1. A value of 0 indicates that the variables are not correlated (McClave and Dietrich, 1982).

The most energetically demanding months for Cebus females are the four months after giving birth, when they are nursing infants. On the chance that month-by-month comparisons might mask differences among reproductive and nonreproductive females, data for all reproductive females were pooled for the four months following parturition and the pooled data were compared to data for the nonreproductive females. The latter data were pooled for a five-month period, since the births took place over a period of two months. Thus the reproductive data for June through September were pooled for females that gave birth in June, the data for July through October for those that gave birth in July, and data for June through October for the nonreproductives.

Data were pooled in two fashions. The aggregated monthly data comprised all observations for the entire period for each animal. Thus, the amount of time one monkey spent feeding in the four months was divided into the total four-

month sample time for that monkey to find a percentage; those percentages were averaged and compared for reproductives and nonreproductives. The combined individual months method used data for each month for each monkey, and combined the monthly averages for a pool of the data for the four-month period. Instead of pooling one data point for each monkey for each activity, as in the aggregate method, this method pools four data points--one for each month--for each reproductive monkey, and five for each nonreproductive, allowing a larger value for  $n$ .

Both the Wilcoxon Rank Sum Test and the Spearman Rank-Order Correlation Test were applied to both sets of pooled data to determine if significant differences existed. A Kruskal-Wallis Test, which yields a Chi-Square Approximation (Schlotzhauer and Littell, 1987), was also performed on the combined individual months data; it could not be used on the aggregated months data because one of its assumptions is that there are at least five observations in each sample. In addition, a General Linear Model (McClave and Dietrich, 1982) was applied to obtain an analysis of variance for both four-month data sets. The General Linear Model was chosen because of the unbalanced samples. It yielded  $r^2$  and  $F$  values. The null hypothesis for the Kruskal-Wallis and Wilcoxon tests was that the sample probability distributions were identical. The null hypothesis for the Spearman tests was that there was no correlation between reproductive state and percentage of time spent on each activity. The null hypothesis for the  $F$  Test

was that the sample variances are equal for the two reproductive states, and the null hypothesis for the T-Test was that the average percentages of time spent on each activity for the two reproductive states were equal. It was expected that differences would show up in the data, allowing rejection of the null hypotheses.

The data were also graphed for the periods of May through August, 1984, and July through December, 1984. The data were subdivided into three categories (nonreproductives, reproductives that lost infants, and reproductives that kept their infants) and graphed by month and by activity. Values for all reproductive animals were combined until August, the first month of data after three females lost their infants. As mentioned above, dividing the data into three categories made the sample sizes too small for statistical analysis, but Silk (in prep.) stressed that it is important to distinguish between females that gave birth to surviving and nonsurviving young. She found in her study that the females who produced nonsurviving young experienced declines in feeding behavior during pregnancy, as well as longer pregnancies than those that reproduced successfully. Graphing of data sometimes reveals patterns, even though they may not be statistically significant.

The data for percent foraging success, average distance of nearest neighbor within 10m and frequency of a neighbor within 10m were also graphed, in case comparisons of those graphs might shed light on the interrelationships between

foraging success and nearness of possible competitors. The data for these graphs were taken from the five-minute instantaneous samples of each animal.

## RESULTS

Statistical results are presented in tabular form in Tables 1-10. The graphic comparisons of the three categories of sample females are presented in Figures 1-15. The raw percentages for each animal for each month comprise the Appendix.

Statistical comparisons made in this study focussed on the differences between activity budgets of reproductive and nonreproductive female capuchins. Graphic comparisons were also made among the activity budgets of three categories of females: nonreproductives, reproductives that lost their infants, and reproductives that kept their infants. The comparisons were made with respect to the following activities: foraging, feeding, moving, lying and sitting.

Statistical comparison of the monthly activity budgets showed no significant differences ( $p < 0.05$ ) with the exception of the data for the category "sitting" in November (Tables 1-4). Analysis of the pooled data for the period of June to October showed no significant differences ( $p < 0.05$ ) (Tables 5-10).

Although the differences between reproductive and nonreproductive females were not significant, certain consistent patterns emerged, particularly in the critical



period from June through October, when the activities were broken into three categories. The three females who lost infants in July consistently spent more time feeding during the four-month period after they lost their infants, and less time moving (Figs. 1 and 3). Overall, they also spent more time foraging (Fig. 2), but the pattern of foraging time vacillated. There appears to be a consistent pattern among those females of trading off foraging and resting times. In months when foraging times were high, resting times were low, and vice versa (Figs. 1 and 4).

In contrast, the females that kept their infants foraged less than either of the other two groups during the critical four-month period, and moved more (Figs. 1 and 3). Neither feeding nor resting activities showed a consistent pattern in those females (Figs. 2 and 4), but there appears to be a pattern of trading off foraging and moving time. In the months when their foraging times were high, moving times were low, and vice versa (Figs. 1 and 3).

The graphs of monthly activities support the patterns discussed above, but do not reveal any other trends (Figs. 5-12). Reproductive females that kept their infants appeared to have consistently higher foraging success than the other two groups, while nonreproductives had consistently lower success rates (Fig. 13). There were no consistent patterns among the three categories of females with respect to the proportion of time another member of the troop was within 10m of the

foraging animal (Fig.14), nor in the average nearest neighbor distances among the three categories (Fig. 15).

### Tables

Table 1. T-test Approximate Significance Values by Month. Values are the result of comparing activities of reproductive to nonreproductive animals for the months of May to December. Values represent the probability of error when rejecting the Null Hypothesis.

|           | FORAGING<br>(11) | FEEDING<br>(22) | MOVING<br>(33) | LYING<br>(44) | SITTING<br>(66) |
|-----------|------------------|-----------------|----------------|---------------|-----------------|
| MAY       | 0.8893           | 0.8893          | 0.6780         | 0.2351        | 0.6780          |
| JUNE      | 0.4939           | 0.6780          | 0.3460         | 0.8655        | 0.6780          |
| JULY      | 0.5573           | 0.7228          | 0.5573         | 0.3460        | 0.9055          |
| AUGUST    | 0.8573           | 0.8573          | 0.3674         | 0.7217        | 0.3674          |
| SEPTEMBER | 0.4162           | 0.4162          | 0.7228         | 0.4939        | 0.7228          |
| OCTOBER   | 0.8261           | 0.8621          | 0.5184         | 0.6026        | 0.2994          |
| NOVEMBER  | 0.5573           | 0.9055          | 0.5573         | 0.2994        | 0.0484          |
| DECEMBER  | 0.7228           | 0.9055          | 0.7228         | 0.4370        | 0.7228          |

Table 2. Sums of Scores. Sums for comparison of reproductive and nonreproductive animals for May to December. These can be compared to rejection regions given in Table 3.

|           | FORAGING           | FEEDING            | MOVING             | LYING              | SITTING            |
|-----------|--------------------|--------------------|--------------------|--------------------|--------------------|
| MAY       | 19, 17<br>(n=4, 4) | 18, 18<br>(n=4, 4) | 20, 16<br>(n=4, 4) | 13, 23<br>(n=4, 4) | 20, 16<br>(n=4, 4) |
| JUNE      | 21, 15<br>(n=4, 4) | 16, 20<br>(n=4, 4) | 22, 14<br>(n=4, 4) | 12, 16<br>(n=3, 4) | 16, 20<br>(n=4, 4) |
| JULY      | 17, 28<br>(n=4, 5) | 22, 23<br>(n=4, 5) | 23, 22<br>(n=4, 5) | 22, 14<br>(n=4, 4) | 19, 26<br>(n=4, 5) |
| AUGUST    | 18, 18<br>(n=3, 5) | 13, 23<br>(n=3, 5) | 8, 28<br>(n=3, 5)  | 15, 13<br>(n=3, 4) | 12, 24<br>(n=3, 5) |
| SEPTEMBER | 24, 21<br>(n=4, 5) | 16, 29<br>(n=4, 5) | 22, 23<br>(n=4, 5) | 15, 21<br>(n=4, 4) | 22, 23<br>(n=4, 5) |
| OCTOBER   | 6, 15<br>(n=2, 4)  | 6, 15<br>(n=2, 4)  | 9, 12<br>(n=2, 4)  | 3, 3<br>(n=1, 2)   | 4, 17<br>(n=2, 4)  |
| NOVEMBER  | 23, 22<br>(n=4, 5) | 20, 25<br>(n=4, 5) | 23, 22<br>(n=4, 5) | 4, 17<br>(n=2, 4)  | 10, 35<br>(n=4, 5) |
| DECEMBER  | 18, 27<br>(n=4, 5) | 21, 24<br>(n=4, 5) | 18, 27<br>(n=4, 5) | 6, 4<br>(n=3, 1)   | 18, 27<br>(n=4, 5) |

Table 3. Rejection Regions for Sums of Scores. Only the value for the lower value of n is used. (From McClave and Dietrich, 1982)

| n2 | n1 | 3              |                | 4              |                | 5              |                |
|----|----|----------------|----------------|----------------|----------------|----------------|----------------|
|    |    | T <sub>l</sub> | T <sub>u</sub> | T <sub>l</sub> | T <sub>u</sub> | T <sub>l</sub> | T <sub>u</sub> |
| 3  |    | 6              | 15             | 7              | 17             | 7              | 20             |
| 4  |    | 7              | 17             | 12             | 24             | 13             | 27             |
| 5  |    | 7              | 20             | 13             | 27             | 19             | 36             |

Table 4. Spearman Rank Sum Correlations by Months. Comparisons are for reproductive versus nonreproductive animals for May to December. The numbers in brackets represent the probability that observed differences for the two sets of values are random.

|           | FORAGING             | FEEDING              | MOVING               | LYING                | SITTING              |
|-----------|----------------------|----------------------|----------------------|----------------------|----------------------|
| MAY       | -0.10911<br>(0.7970) | 0.00000<br>(1.0000)  | -0.21822<br>(0.6036) | 0.54554<br>(0.1619)  | -0.21822<br>(0.6036) |
| JUNE      | -0.32733<br>(0.4287) | 0.21822<br>(0.6036)  | -0.43644<br>(0.2797) | 0.00000<br>(1.0000)  | 0.21822<br>(0.6036)  |
| JULY      | 0.25981<br>(0.4996)  | 0.17321<br>(0.6559)  | -0.25981<br>(0.4996) | -0.43644<br>(0.2797) | 0.08660<br>(0.8247)  |
| AUGUST    | -0.50709<br>(0.1996) | 0.05634<br>(0.8946)  | 0.61978<br>(0.1012)  | -0.43301<br>(0.3318) | 0.16903<br>(0.6891)  |
| SEPTEMBER | -0.34641<br>(0.3611) | -0.34641<br>(0.3611) | -0.17321<br>(0.6559) | 0.32733<br>(0.4287)  | -0.17321<br>(0.6559) |
| OCTOBER   | 0.20702<br>(0.6939)  | 0.20702<br>(0.6939)  | -0.41404<br>(0.4144) | -0.86603<br>(0.3333) | 0.62106<br>(0.1882)  |
| NOVEMBER  | -0.25981<br>(0.4996) | 0.00000<br>(1.0000)  | -0.25981<br>(0.4996) | 0.62106<br>(0.1882)  | 0.86603<br>(0.0025)  |
| DECEMBER  | 0.17321<br>(0.6559)  | -0.08660<br>(0.8247) | 0.17321<br>(0.6559)  | 0.77460<br>(0.2254)  | 0.17321<br>(0.6559)  |

Table 5. T-test Approximate Significance Values for Pooled Data. Values are the result of comparing both aggregated monthly data and combined individual monthly data for reproductive animals for the four months following births with data for the nonreproductive females over the same time. Values represent the probability of error when rejecting the null hypothesis.

|           | FORAGING | FEEDING | MOVING | LYING  | SITTING |
|-----------|----------|---------|--------|--------|---------|
| AGGREGATE |          |         |        |        |         |
| MONTHLY   | 0.4162   | 0.7228  | 0.3024 | 0.5573 | 0.9055  |
| DATA      |          |         |        |        |         |
| COMBINED  |          |         |        |        |         |
| INDIVID.  | 0.1115   | 0.4059  | 0.9869 | 0.2388 | 0.4828  |
| MONTHS    |          |         |        |        |         |

Table 6. Sums of Scores for Aggregated Monthly Data. Sums for comparison of reproductive and nonreproductive females for the first four months after births. Sums are for aggregated monthly data only. These can be compared to rejection regions given in Table 3. Only the value for the lower value of n is used.

|           | FORAGING | FEEDING | MOVING  | LYING   | SITTING |
|-----------|----------|---------|---------|---------|---------|
| AGGREGATE |          |         |         |         |         |
| MONTHLY   | 24,21    | 18,27   | 15,30   | 23,22   | 21,24   |
| DATA      | (n=4,5)  | (n=4,5) | (n=4,5) | (n=4,5) | (n=4,5) |

Table 7. Kruskal-Wallis Test (Chi-Square Approximation) Values. Values result from comparing data for reproductive and nonreproductive females, using pooled data from combined individual months. Probability > Chi-Square (in brackets) gives the probability of making an error if the null hypothesis is rejected.

|            | FORAGING           | FEEDING              | MOVING              | LYING              | SITTING             |
|------------|--------------------|----------------------|---------------------|--------------------|---------------------|
| CHI-SQUARE |                    |                      |                     |                    |                     |
| VALUES     | 2.7233<br>(0.0989) | 0.773638<br>(0.3908) | 0.00109<br>(0.9737) | 1.4972<br>(0.2211) | 0.52723<br>(0.4678) |

Table 8. Spearman Rank Sum Correlations for Pooled Data. Values are the result of comparing both aggregated monthly data and combined individual monthly data for reproductive animals for the four months following births with data for the nonreproductive females over the same period. The numbers in brackets represent the probability of error when rejecting the null hypothesis.

|           | FORAGING | FEEDING  | MOVING   | LYING    | SITTING  |
|-----------|----------|----------|----------|----------|----------|
| AGGREGATE |          |          |          |          |          |
| MONTHLY   | -0.34641 | 0.17321  | 0.43301  | -0.25981 | -0.08660 |
| DATA      | (0.3611) | (0.6559) | (0.2443) | (0.4996) | (0.8247) |
|           | (n=9)    | (n=9)    | (n=9)    | (n=9)    | (n=9)    |
| COMBINED  |          |          |          |          |          |
| INDIVID.  | -0.28301 | 0.14717  | -0.00566 | -0.22722 | 0.12453  |
| MONTHS    | (0.0995) | (0.3989) | (0.9743) | (0.2272) | (0.4760) |
|           | (n=35)   | (n=35)   | (n=35)   | (n=30)   | (n=35)   |

Table 9.  $R^2$  and F Values for Aggregated Monthly Data. Values are the result of comparing reproductive females during the first four months following births with nonreproductive females over the same period. Probability>F (in brackets) gives the probability of making an error if the null hypothesis is rejected.

|              | FORAGING | FEEDING  | MOVING   | LYING    | SITTING  |
|--------------|----------|----------|----------|----------|----------|
| $r^2$ VALUES | 0.103080 | 0.003268 | 0.172905 | 0.118806 | 0.000912 |
| F VALUES     | 0.80     | 0.02     | 1.46     | 0.94     | 0.01     |
| AND          | (0.3996) | (0.8839) | (0.2657) | (0.3637) | (0.9385) |
| PROB>F       |          |          |          |          |          |

Table 10.  $R^2$  and F Values for Combined Individual Months. Values are the result of comparing reproductive females during the first four months following births with nonreproductive females over the same period. Probability>F (in brackets) gives the probability of making an error if the null hypothesis is rejected.

|              | FORAGING | FEEDING  | MOVING   | LYING    | SITTING  |
|--------------|----------|----------|----------|----------|----------|
| $r^2$ VALUES | 0.035259 | 0.015947 | 0.014912 | 0.038683 | 0.061518 |
| F VALUES     | 1.21     | 0.53     | 0.50     | 1.13     | 2.16     |
| AND          | (0.2801) | (0.4698) | (0.4847) | (0.2975) | (0.1508) |
| PROB>F       |          |          |          |          |          |

## Graphs

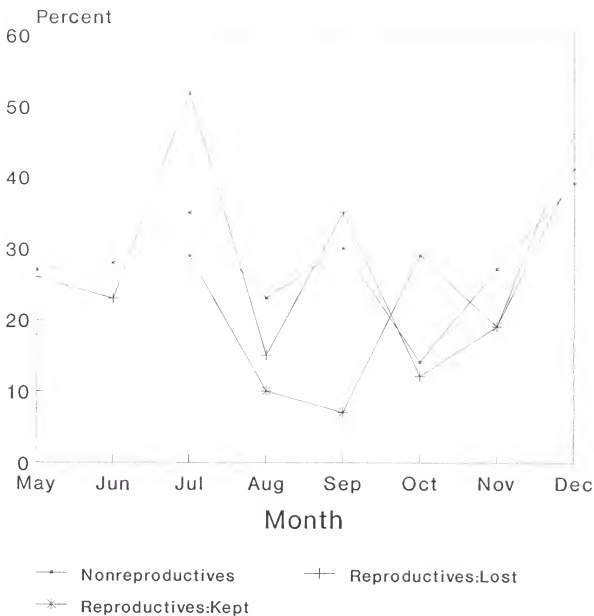


Figure 1. Foraging Times by Groups. Percentage of total time devoted to foraging for each group (nonreproductives, reproductives that kept infants and reproductives that lost infants) from May to December.



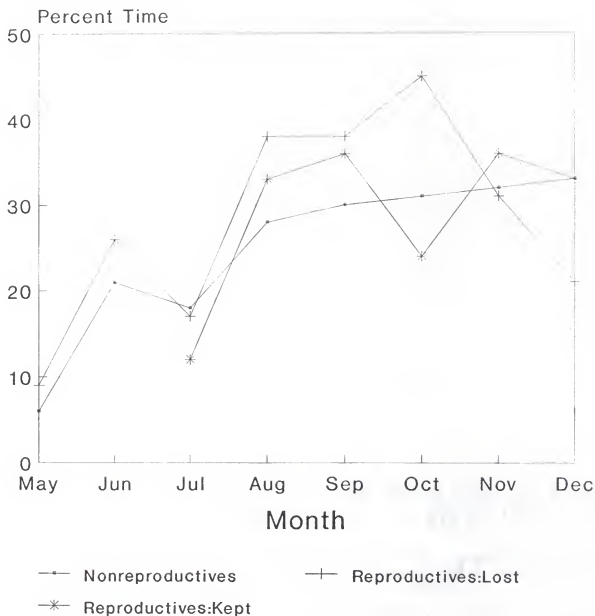


Figure 2. Feeding Times by Groups. Percentage of total time devoted to feeding for each group (nonreproductives, reproductives that kept infants and reproductives that lost infants) from May to December.

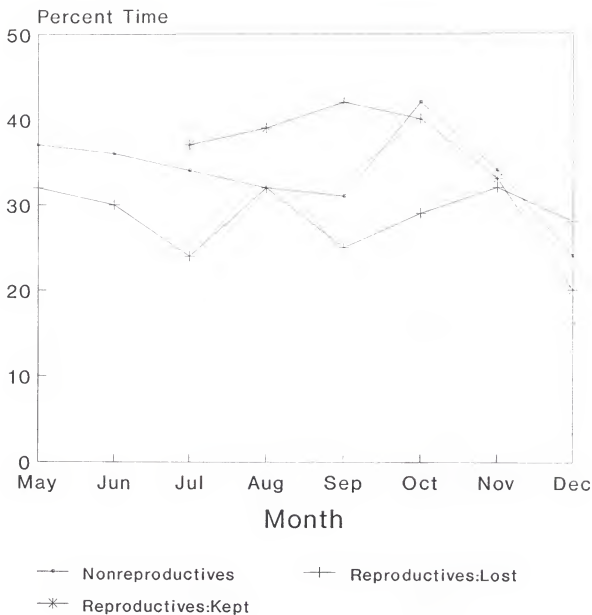


Figure 3. Moving Times by Groups. Percentage of total time devoted to moving for each group (nonreproductives, reproductives that kept infants and reproductives that lost infants) from May to December.

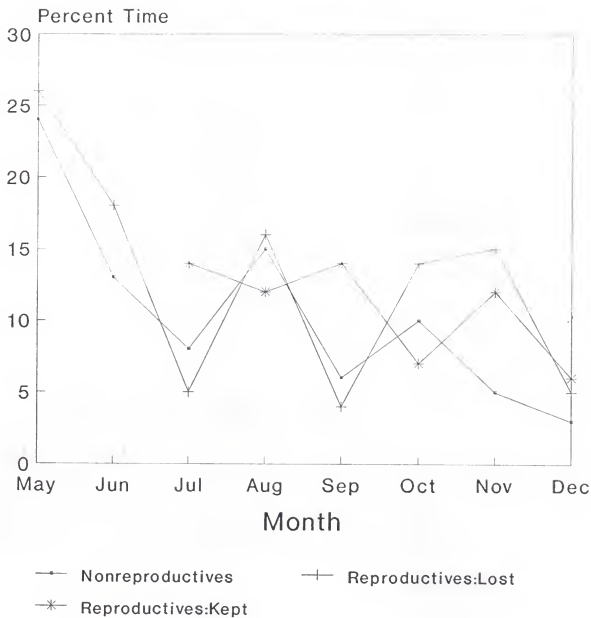


Figure 4. Resting Times by Groups. Percentage of total time devoted to resting (lying and sitting) for each group (nonreproductives, reproductives that kept infants and reproductives that lost infants) from May to December.

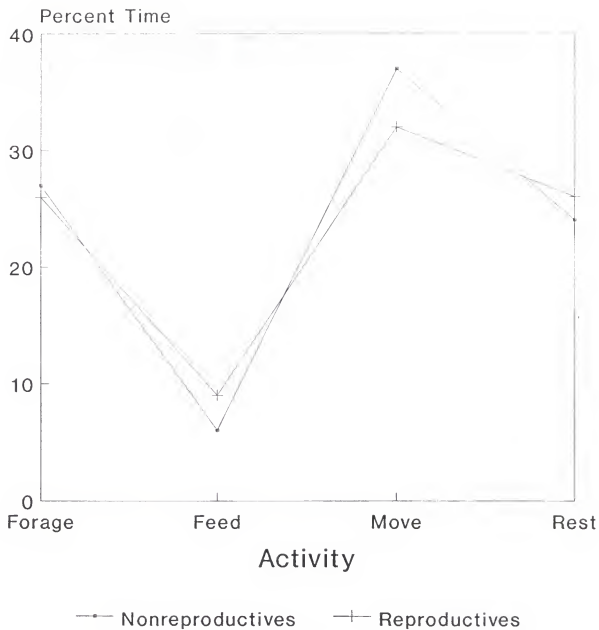


Figure 5. May Activities. Percentage of total time devoted to major activity categories by each group in May.

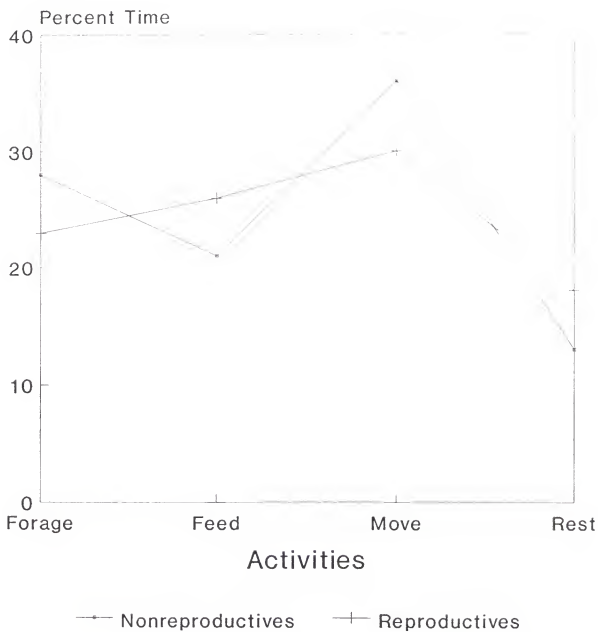


Figure 6. June Activities. Percentage of total time devoted to major activity categories by each group in June.

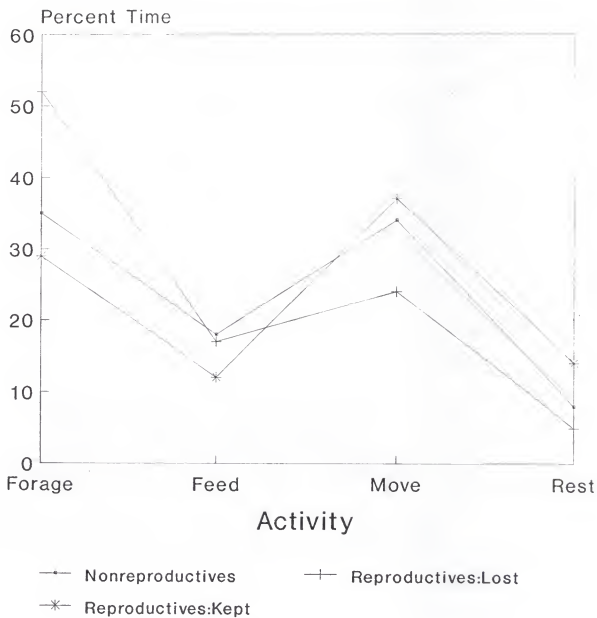


Figure 7. July Activities. Percentage of total time devoted to major activity categories by each group in July.

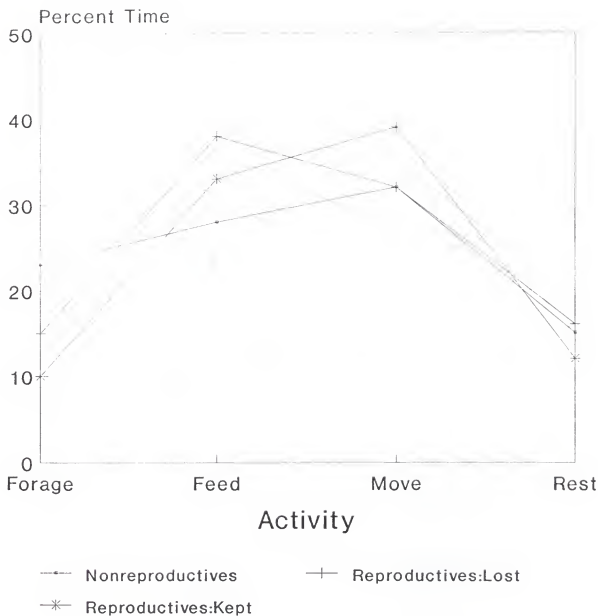


Figure 8. August Activities. Percentage of total time devoted to major activity categories by each group in August.

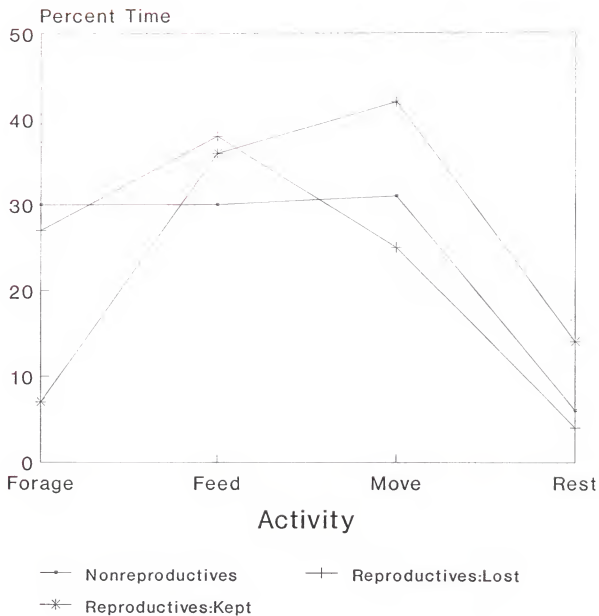


Figure 9. September Activities. Percentage of total time devoted to major activity categories by each group in September.



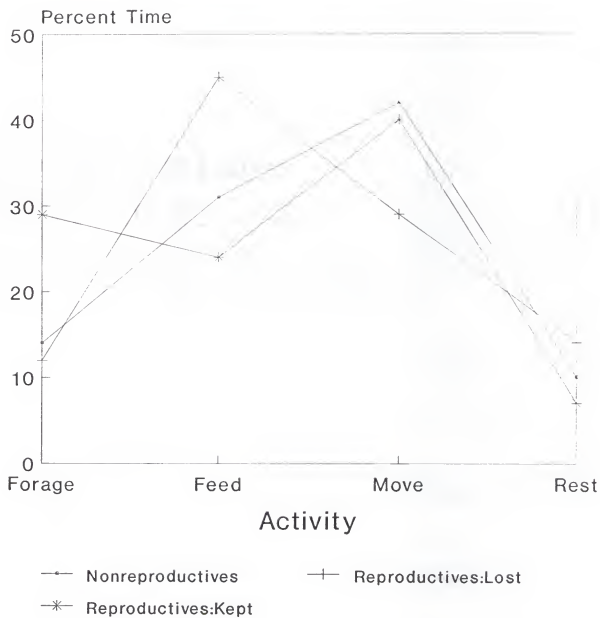


Figure 10. October Activities. Percentage of total time devoted to major activity categories by each group in October.

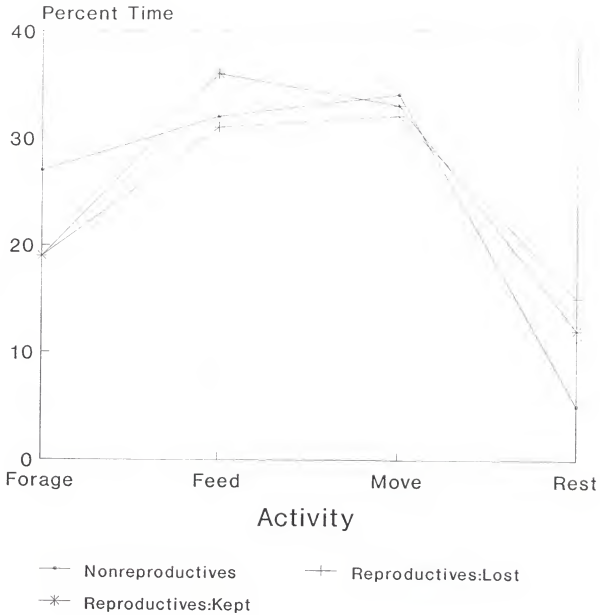


Figure 11. November Activities. Percentage of total time devoted to major activity categories by each group in November.

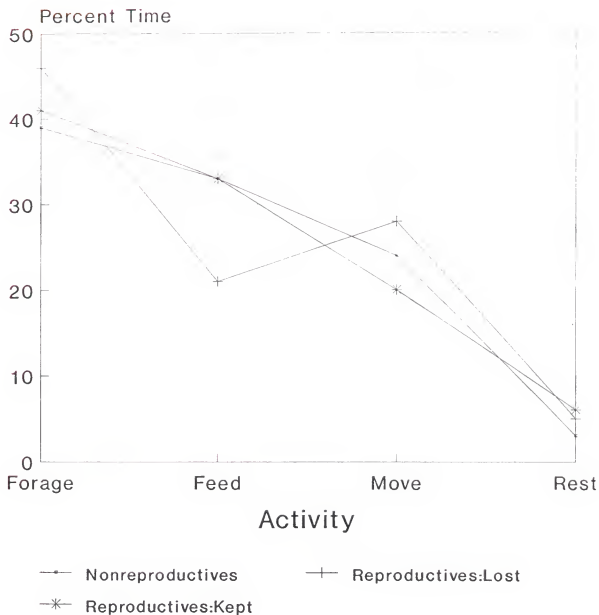


Figure 12. December Activities. Percentage of total time devoted to major activity categories by each group in December.

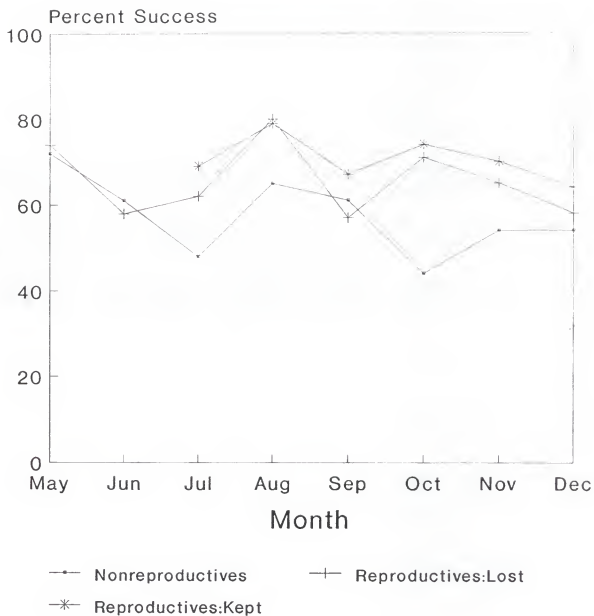


Figure 13. Foraging Success. Percent success foraging by each group from May through December.

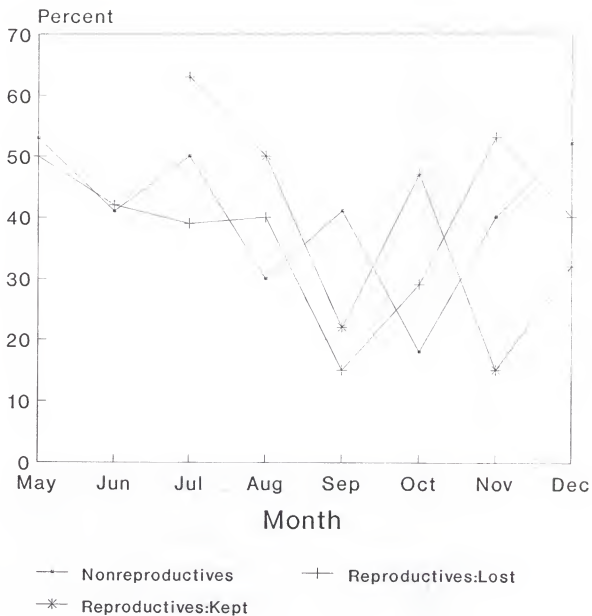


Figure 14. Neighbors. Percent of time neighbor was within 10m of each sample animal while foraging

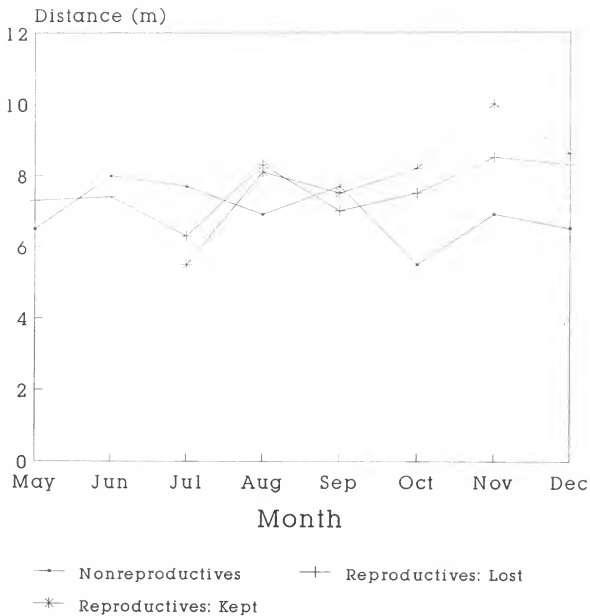


Figure 15. Nearest Neighbor Distance. Average distance of nearest neighbor (within 10m) to each sample animal as it was foraging.

## DISCUSSION AND CONCLUSIONS

### Discussion

The data do not show significant differences between the time budgets of reproductive and nonreproductive females in Main Group. The single instance of a significant value is for sitting in November, but it is somewhat of an anomaly, and is not reinforced by the values for sitting in any other month. The values for foraging in Table 7 and Table 8 (chi-square and Spearman values, respectively) are of interest, because they are significant at a 90% confidence level. Foraging, which largely involves searching for invertebrates, is the aspect of feeding behavior that contributes most directly to the sample animals' protein budgets. If foraging time budgets were in fact significantly different, it might represent an effort to increase protein levels. This is interesting in the light of the trends for increased feeding time and an apparent tradeoff between foraging time and moving time among the females who lost their infants. It might be expected that females that lost infants would increase their food intake in an effort to reach a nutritional level sufficiently high to breed in the next year, rather than following the usual two-year cycle. In fact, all three of the females who lost infants did recycle and produce infants in the following year.

However, only two of the five tests performed on the combined individual monthly foraging data showed significance even at the 90% level. While it would be wrong to dismiss the foraging results out of hand, in light of the conflicting results of the other three tests and the low level of confidence, there must be considerable question as to the relevance and acceptability of the measures. At the 95% confidence level at which the data were tested, no significant differences between reproductive and nonreproductive females occurred. Therefore, the null hypothesis, that there are no differences between the two groups, cannot be rejected.

Since it was expected that differences in energy budgets would be reflected in the activity schedules of the two groups of females, this lack of corroboration is somewhat surprising. The explanation appears to lie in a combination of factors, among which is the unusual situation of the study group.

Robinson (1986) recorded no significant differences in foraging between lactating and nonlactating female capuchins in the study group. During dry season months, though, corresponding to the early or middle months of pregnancy in the capuchins, he found significant differences in foraging between pregnant and nonpregnant females. Boinski (1988) found few differences between the foraging behaviors of reproductive and nonreproductive squirrel monkeys, animals that overlap ecologically with capuchins to a considerable



degree (Terborgh, 1983; Eisenberg, 1989). However, Boinski does not offer an explanation for the lack of differences.

Altmann (1980) found that in approximately 90 percent of her samples of baboons, reproductive animals' predominant activities were the same as those of the group as a whole. The bulk of the deviation occurred in the first month after birth when there was only 80% concordance, and particularly on day one of infant life, when there was only 60% concordance, presumably because of the animals' need for additional resting time immediately after giving birth. Altmann explained the concordance in activities by suggesting that reproductive animals may be incurring an energy debt.

There are several other possible explanations for the lack of differences between the two categories of females in the study group. The first possibility is that the differences exist but were not detected in the small samples represented in this study. This could happen if variation between individuals swamped the variation between reproductive categories. O'Brien (1990), working with the same study animals, noted considerable variation in the activity of each individual. With such small numbers, statistical analysis at a meaningful level is difficult.

On the other hand, if the data accurately reflect the real situation, then capuchin females do not alter their time budgets to accommodate the energetic demands of pregnancy. If that is the case, they must be coping with the energetic demands in other ways. One possibility is that pregnant and

lactating females simply increase their foraging efficiency. The graph of foraging efficiency for the three groups of sample animals does not support this explanation, but the argument can be considered on the basis of several other factors. Although considered ripe-fruit specialists, capuchins derive a considerable amount of their caloric input, especially protein, from invertebrates (Robinson, 1981). Females rely somewhat less on this source than males (Fragaszy, 1986; note contrast to Gautier-Hion, 1980), but still spend large amounts of time foraging for invertebrates and the occasional vertebrate (I have observed females eating murid opossums and frogs on several occasions).

However, as Robinson (1981) has pointed out, evenly dispersed, small invertebrates are not a resource that is monopolizable; the potential benefit from any one food unit is less than the cost of defending it or seizing it. It would be difficult to increase foraging efficiency for these items, except through experience, which could just as easily apply to all animals.

Altmann's (1980) maternal feeding time model assumes feeding efficiency to be constant, but considers a number of factors, predominantly social, that might obviate that assumption. A factor not considered in the model is that the presence of an infant might lower the efficiency of a female (Wright, 1984). Altmann describes females with infants as foraging less efficiently. Again, it is difficult to see how feeding efficiency could be significantly improved; it is

more likely that females with infants forage less efficiently, since both their physical effort and attention must be divided between foraging and the needs of the infant.

Intuitively, also, the assumption of improved feeding efficiency for reproductive females raises some problems. The most obvious of these is: if females can raise their feeding efficiency during reproductive periods, it would be to their benefit to do it all the time. Thus, the differences between reproductive and nonreproductive females would be cancelled. Alternatively, there could be undocumented costs--such as increased risk of predation--to such an increase in efficiency that reproductive females are willing to pay. Robinson (1981) has argued that males pursue such a strategy, foraging more frequently on the ground at a greater risk.

The strongest argument against an improved-efficiency hypothesis is that food does not seem to be a limiting factor during the last months of pregnancy and the first few months of lactation. Like many primates (Napier and Napier, 1985), Cebus olivaceus at the study site have a fairly well-defined birth season, ranging from May to October, but with the largest number of births occurring in June and July (Robinson, 1988). These are peak months of habitat productivity, when fruits are at their most abundant and major invertebrate productivity pulses, such as caterpillar flushes and leafcutter ant flights, provide bonanzas of protein and fat.

Robinson (1986) suggests that among the study animals young and middle-aged females follow a two-year reproductive cycle, although there are instances when females have produced infants in successive years and when they have skipped years. Older females show a greater gap (almost four years, on average) between infants (Robinson, 1988b). A female that has lost an infant in one breeding season is more likely to become pregnant the next year than one whose infant has survived. A variety of studies demonstrates a seasonal breeding pattern in primates such as Macaca sylvana (MacRoberts and MacRoberts, 1966), Erythrocebus patas (Johnston and Rowell, 1987), Saimiri sciureus (Coe & Rosenblum, 1978; Baldwin, 1970), Miopithecus talapoin (Rowell, 1977), various prosimians (Rasmussen, 1985), Cercocebus albigena (Rowell and Chalmers, 1970), Macaca mulatta (Conaway and Koford, 1964), Cercopithecus mitis (Omar and De Vos, 1971), Homo sapiens (Ehrenkranz, 1983), Papio cynocephalus (Altmann et al., 1977) and others. General discussions of the subject include Lancaster and Lee (1965), Vandenbergh and Vessey (1968) and Rowell and Richards (1979).

The question of seasonality should be kept distinct from the related question of interbirth intervals. Harvey, et al. (1987) point out that primate interbirth intervals, with some exceptions, are correlated to adult body size and adult body weight. They go on to suggest that primates living in seasonal environments would be expected to fine-tune their breeding efforts to produce young at the period of maximum

food availability. Working with sheep, Karsch and Foster (1981) demonstrated that a decrease in response to oestradiol inhibition of tonic LH secretion can act as a final mechanism for such fine tuning. Using figures for rhesus monkeys on La Parguera Island, Follett (1984) found that mortality rises as births shift away from the median birth date for the group. Seasonality in breeding seems to be a response to relatively predictable seasonality in local climate or availability of resources. According to Rowell and Richards (1979) the ultimate selection pressure for seasonal mammalian reproductivity lies in the presence of a food supply for lactating mothers. Keverne (1987) lays more stress on social factors as proximal causes of primate reproductive cycles, but is careful to emphasize the role of food availability, as well. Gautier-Hion (1968) has mentioned other climate-related factors, particularly cold weather, which might affect the survivorship of young animals. Cold is less likely to be a factor in the case of the study animals, which live at low altitude, 8 degrees from the equator. However, young monkeys can be chilled by night-time rainstorms and suffer from exposure (pers. obs.).

A wider variety of explanations has been put forth for the proximate factors leading to seasonal breeding patterns. In general, these fall into two categories. The first are outside factors that cue reproductive behavior, such as day length or rainfall. Kawai et al. (1967) reported significant differences in the timing of the birth season among

geographically varied troops of Macaca fuscata, suggesting an environmental explanation, although no direct correlation could be established. Bronson (1989) has suggested also that "some facet of the energetic cost/gain ratio of foraging" might act as a potential predictor of seasonal change, cueing reproductive activity. Since the site of this study is so close to the equator, day length does not seem to be a prime candidate as a reproductive cue; although reproductive activity takes place during the shortest days of the year, the difference is very slight (less than 30 minutes). Similarly, rainfall can be ruled out, since the short days are in the middle of the dry season. If a lack of rainfall is a cue, then it seems more likely to act indirectly, through the food ingested by the animals. Bronson's suggestion concerning a cost/gain foraging ratio would be extremely difficult to prove and seems at first glance to be a rather sophisticated and roundabout mechanism for cueing a behavior pattern. It is also possible that the proximate factor lies in a combination of several factors: day length, vegetation changes, lack of rainfall, decreased foraging efficiency and others. However, as Ward (1969) has pointed out, a response to such a complicated set of circumstances would be difficult to evolve and difficult to prove.

The second category is internal clues, such as general nutritional level or the presence of an adequate amount of one or more crucial nutrients or compounds that would serve as reproductive cues. As mentioned in the introduction,

nutritional levels have been shown to be important factors in primate reproduction (see also Sadleir, 1969; Frisch and McArthur, 1974; Lee, 1987; Gilmore, 1981). Studies on bats (Barclay, 1989), squirrels (Wauters and Dhondt, 1989) and red deer (Albon et al., 1983), among others, have also stressed the importance of maternal nutrition.

A number of researchers have focussed on protein as the crucial nutrient most likely to affect reproduction in mammals, although calcium and a variety of other nutrients have also been found necessary for deer (Verme and Ullrey, 1984). There is a considerable body of literature to support the importance of protein in white-tailed deer reproduction (e.g., Cheatum and Severinghaus, 1950; Murphy and Coates, 1967; Verme, 1969; Richter and Labisky, 1985). As mentioned in the introduction, protein levels have been shown to be crucial to reproductive female primates (see also Ausman, 1973, and Flurer and Zucker, 1985). Gautier-Hion (1980) has shown that female Cercopithecus monkeys reorient their food choice to increase protein intake when pregnant or lactating. Protein has been shown to be a critical nutrient for birds, as well (e.g., Jones and Ward, 1976; Fogden, 1972).

Jameson (1988) has discussed the role of secondary plant compounds as both instigators and inhibitors of reproductive activity; many of the studies of this effect have been on domestic livestock. The effects of these compounds (generally referred to as phytoestrogens) on wildlife have been documented in a number of studies (e.g., Leopold, et

al., 1976; Berger, et al., 1977; Negus and Berger, 1977). In a significant effort, Whitten (1983) has demonstrated a link between reproduction and the occurrence of Acacia elatior flowers for Cercopithecus aethiops, in the Samburu-Isiolo Game Reserves, in Kenya. Early occurrence and use of the flowers were related to earlier onset of mating; longer availability and use of the flowers related to longer mating and birth seasons. Whitten speculates that the flowers may have affected the onset of mating in three ways. Flower consumption may have led to weight gains that triggered ovulatory activity. Second, the flowers may have contained essential nutrients, such as the trace elements discussed by Kaminetsky and Baker (1980) and mentioned in Chapter One. Third, Whitten speculates that the presence of estrogen-like compounds in the flowers may have brought the females who ate them into reproductive condition. In a later paper, Whitten (1984) points out that exploitation of the genus Acacia may be an important part of the vervet feeding niche and speculates that the consumption of Acacia flowers may serve to synchronize vervet births with Acacia fruiting, providing critical nourishment for lactating females.

A series of papers (Negus and Berger, 1977; Butterstein, et al., 1985; Berger, et al., 1987; Schadler, et al., 1988) has established that a plant metabolite, 6-methoxybenzoxazolinone, stimulates reproductive activity and causes an increase in the weight of reproductive organs in microtine



rodents. Bronson (1989) has mentioned the possibility of chemical compounds in insects acting as cues for predators.

Robinson (1986) has suggested that the largest limiting factor in food intake among the study group during peak periods is the speed of their digestion. There is literally more food than they can eat at many times during these months. At such times feeding efficiency is a moot point. The critical period for the study animals comes during the dry season, when they are forced to rely heavily on sporadic and presumably unpredictable episodes of fruiting by fig trees and the day-to-day utilization of palm trees. It is at this time, the most stressful for the animals, that the females conceive.

Obviously, the ultimate selecting factor for seasonality in Cebus reproduction is that the young are thus born and nursed at a time of maximum resource availability, giving them a better chance of survival. The proximate causes are less obvious, although rainfall would seem to be ruled out and day length so close to the equator seems questionable. It seems more likely that the proximate factor is nutrition-related in some fashion.

In the case of the study group, another factor may be strongly affecting the situation, raising the overall level of food--and thus energy--available year around to the study animals. The study site at Masaguaral, while retaining its gallery forest relatively intact, has a less diverse fauna--particularly in the primate community--than other Neotropical

sites that have been studied. Interspecies competition for food resources may thus be at a significantly lower level than at other primate study sites. Gautier-Hion (1980) has suggested that among species of Cercopithecus monkeys sharing a habitat, interspecific competition is an important determinant of resource partitioning. The importance of this can be seen by comparing species composition at the study site with those at other documented sites (Table 11).

Terborgh (1983) compared estimates of mammalian frugivore biomass at three Neotropical forest localities, using his own data from Cocha Cashu, Peru, data from Eisenberg, et.al. (1979) for Guatopo, Venezuela, and from Eisenberg and Thorington (1973) for Barro Colorado Island, Panama. Of these, only Cocha Cashu can be considered undisturbed, and Terborgh is careful to point out the problems of comparing the sites. Nevertheless, the most striking aspect of the comparison is the biomass of primates at Cocha Cashu (650kg/km, compared to 421kg for BCI and 167kg at Guatopo) and the much greater percentage (57%) of arboreal frugivores there than at the other two sites (37% and 29% respectively). Additionally, Terborgh reports 11 primate species within the study site, and two more in nearby forest, a figure confirmed by Janson and Emmons (1990). By comparison, Guatopo, a semi-deciduous forest with hunting pressure, has three primates and Barro Colorado has five (Eisenberg and Thorington, 1973; Glanz, 1990). At each of the latter sites, species of Cebus share the habitat with either

Table 11. Numbers of Primate Species Recorded at Selected Sites in the Neotropics.

| SITE                          | NUMBER OF PRIMATE SPECIES RECORDED | SOURCE                        |
|-------------------------------|------------------------------------|-------------------------------|
| Cocha Cashu, Peru             | 11                                 | Terborgh (1983)               |
| Guatopo, Venezuela            | 3                                  | Eisenberg, et al., (1979)     |
| Barro Colorado Island, Panama | 5                                  | Eisenberg & Thorington (1973) |
| Chiriqui, Panama              | 3                                  | Baldwin & Baldwin (1976)      |
| Santa Rosa, Costa Rica        | 3                                  | Freese (1976)                 |
| La Selva, Costa Rica          | 3                                  | Wilson (1990)                 |
| La Macarena, Colombia         | 7                                  | Izawa (1979)                  |
| MCSE Site, Brazil             | 6                                  | Malcom (1990)                 |

Ateles, which Eisenberg (1989) has described as "primarily frugivorous," or Saimiri, which "feeds primarily on insects and fruit," overlapping the niche of Cebus. Robinson and Janson (1986) have pointed out, however, that the feeding strategies of Saimiri vary with location; thus they may be more or less competitive with capuchins in different areas. Furthermore, although Alouatta is often described as a folivore, Eisenberg (1973, 1979) describes it as a folivore/frugivore, and notes that leaves actually account for only about 40% of the diet of Alouatta seniculus in Venezuela.

Eisenberg, et al. (1979) listed three species of primates at Guatopo, Wilson (1990) listed three species for La Selva, in Costa Rica, and Malcom (1990) listed six primates for the Minimum Critical Size of Ecosystems reserve north of Manaus, Brazil. Izawa (1979) reported seven primate species at his study site in La Macarena National Park in Colombia, including both Ateles and Saimiri. Other studies (e.g. Freese, 1976; Baldwin and Baldwin, 1976; Eisenberg and Thorington, 1973) have also taken place in forests with a minimum of three species that relied on fruit for a major part of their diet. Saimiri, in particular, are known to form mixed groups with Cebus (Terborgh, 1983). Although factors such as elevation, maturity of forest and degrees of disturbance make direct comparisons among all these sites tenuous, the trend is clear: in all other sites studied, at least three fruit-eating primates are found in the forest communities. In contrast, the Masaguaral capuchins have only howler monkeys as primate competitors for fruit.

As a number of researchers have pointed out (e.g., Terborgh, 1983), primates relying on insects for a significant portion of their caloric intake tend to use different methods of capture. Cebus are destructive searchers, relying on their greater strength (compared to other insect-eating primates in their geographical range) to pry, tear, break or strip vegetation in search of hidden invertebrates or small vertebrates. Thus, they are probably

not in significant competition with other omnivorous or insectivorous primates for their protein sources.

Masaguaral's array of nonprimate arboreal frugivores--potential competitors--is somewhat limited. Of the marsupials, only Didelphis marsupialis and Marmosa robinsoni are found in the forest. Procyon cancrivorus, the crab-eating raccoon, the only procyonid found at Masaguaral, is seen only rarely on the study site and Eira barbara, a frugivorous carnivore, is present only in relatively low densities (Eisenberg, 1979), although Robinson (1984) reports that figs at the study site are heavily used by bats, tayras and opossums. Among arboreal rodents, both Coendu prehensilis and Sciurus granatensis are fruit-eaters, but neither occurs in sufficient numbers or biomass (Eisenberg, et al., 1979) to be considered a serious competitor to the capuchins. Indeed, since Sciurus and Marmosa are among the vertebrates eaten by Cebus (Robinson, 1986), their contributions in the form of protein could conceivably outweigh their competitive impact. Among smaller frugivorous rodents, densities of Rhipidomys sp. and Oryzomys bicolor are unknown, but Eisenberg, et al. (1979) list the ecological density of Echimys semivillosus on the site at 40 per square kilometer.

Among the 42 species of bats listed by Eisenberg, et al. as occurring at Masaguaral, 20 are of the family Phyllostomatidae. Of these, at least 17 are considered mildly to strongly frugivorous (Eisenberg, 1989). Eisenberg reports

that Artibeus jamaicensis, the most common of the bats on the site, feeds on Ficus, a mainstay of the Cebus, to the extent that its reproductive timing is closely tied to the maximum fruiting of the genus. It is difficult to estimate the degree of overlap in feeding niches and consequent competition between bats and Cebus on the site. Carollia perspicillata, for instance, is described by Eisenberg (1989) as depending on the fruit of Piper for the major portion of its diet, but Robinson (1986) does not list Piper among the foods eaten by Cebus on the study site. It seems safe to assume considerable overlap between the bats and monkeys, but without further data on numbers and feeding habits of the bats, it is impossible to assess their impact on Cebus. There is also no way to estimate the competitive impact of frugivorous birds at the site, although Morton (1979) describes the use of fruit, especially Ficus, by llanos birds at Masaguaral as extensive.

Another significant factor is that a number of potential predators on Cebus are either missing or found in very low densities at Masaguaral. The importance of predation to primate groups has been stressed by a number of researchers (e.g., van Schaik and van Noordwijk, 1989; Terborgh, 1983; Emmons, 1984; Freese, 1978). Terborgh has stated that "...aerial predators constitute the only serious daytime threat to arboreal primates." However, the largest Neotropical avian predators, the harpy eagle and the crested eagle, have not been recorded in recent times at Masaguaral.

These are the only species recorded to have preyed on Cebus at Cocha Cashu. Terborgh qualifies the above statement by mentioning the possibility of ground predation by Eira barbara or felids. At Masaguaral, at least, tayras do not seem to be regarded as a threat by the monkeys themselves. On one occasion, I watched two tayras move directly through a foraging group of capuchins without raising a warning call; many of the monkeys on the ground did not even look up as they went by. However, Norris (1990) has suggested that tayra/capuchin interactions may be context-sensitive. In over ten years of research, no instance of predation on Cebus has been recorded at Masaguaral, although animals have disappeared. Robinson, in Cheney and Wrangham (1987) has estimated that there have been fifteen instances of predation at the study site since the start of his original study. Ninety percent of those incidents involved infants or juveniles. It is likely that any predation on the monkeys would be nocturnal, coming from boas (Chapman, 1986) or felids. Cebus habitually exhibit a form of mobbing behavior when encountering a boa, although their reaction to rattlesnakes is much more subdued. Animals in the rattlesnake's immediate vicinity may give alarm calls, but the group as a whole seems relatively unconcerned (pers. obs.). Ocelots elicit strong alarm calls from the monkeys, and on the two or three occasions when domestic dogs wandered into the study area, the monkeys not only gave alarm calls, but immediately fled the area. Pumas are recorded for the

site (Eisenberg, 1979), and I often saw their tracks, but never witnessed an encounter between one and a group of monkeys. There is one reported sighting of a jaguar at the site, but it has not been confirmed.

A final factor is Main Group's position among the primate community at Masaguaral. If dominance is defined as having priority at a choice feeding site, then Cebus were generally dominant over the larger, but slower, Alouatta, which habitually occurred in smaller groups. Among the groups of Cebus that habituated the study site, Main Group was the dominant group (Robinson, 1986). In effect, Main Group had uncontested access to those major clumped resources, primarily ripe fruit trees, that could be monopolized. Cheney and Seyfarth (1987) noted that "primate groups are often larger than might be predicted from a consideration of within-group competition alone." They suggested that the explanation lay in a food-defense hypothesis. They further suggested that increased reproductive success among females of large groups of vervet monkeys is due to the increased food resources available to members of a large group. Both Srikosamatara (1987) and Robinson (1988a) have demonstrated that the animals in Main Group were able to increase their feeding efficiency by their ability to displace smaller groups, although Srikosamatara pointed out that it was difficult to prove that these benefits offset the costs of intragroup competition in the larger group.



The overall result of these factors is that Main Group was in an unusual situation where it had very little competition for resources, and apparently low predation pressure. In addition, the group was never in the position of having to waste time and energy by relinquishing a food source and being forced to find another. The net result was that for Main Group, the good times were better and the bad times less bad than for any other Cebus group in the study area. More importantly, the unusual conditions at Masaguaral put Main Group in a situation somewhat removed from those of Cebus living in less disturbed habitats.

Another explanation for the lack of differences in activity schedules is that pregnant and lactating females may deal with their increased caloric demands simply by losing--or at least not gaining--weight. As mentioned in the introduction, it is known that in many primate species a female must reach a certain minimum level of physical fitness, generally reflected in the amount of body fat, before she will reproduce. This implies that reproductive females are not meeting their entire caloric needs by feeding and foraging (but see Millar, 1975 and 1977).

Dunbar (1984) observed that low-ranking gelada baboons seemed to build up an energy debt during the early months of reproduction, which required them to feed at higher levels for longer than high-ranking females. Altmann (1980) found that feeding time for reproductive females was below that predicted by the model. She suggested that weight loss in the

animals was the primary explanation, that the animals operated at times on an energy debt. The concept of an energy debt may be another key to explaining the reproductive strategy of the study animals, as explained below.

The most likely explanation for the lack of differences in time budgets between the two groups of females is a combination of intrinsic factors and conditions specific to the study site. These factors would operate through the following scenario.

A typical Cebus female would have a reproductive year followed by a recovery year, when her infant was still partly dependent. During the wet season, reproductive animals would be able to offset their energetic costs by taking advantage of the superabundance of food without altering their feeding and foraging schedules. Nonreproductives would be storing up fat and/or other nutrients, such as protein, in preparation for breeding the next year. Rather than losing weight, the reproductives would simply not gain as much as the nonreproductive females. During the last few months of lactation, when demands are highest, they would still have strong reserves to draw on without having to alter their activity schedules. Females losing infants or those in exceptionally good health could cycle again the next year (Altmann et al., 1978; Hauser and Fairbanks, 1988), as three of the study animals did. Others, for nutritional reasons, might skip more than one year. The irregularity of the observed pattern in the study group is an indicator that

nutrition is the critical factor. Robinson found some differences in feeding and foraging behavior in the dry season, although this study did not. Such differences may depend on the severity of the dry season. Under this scenario, females may be making up the costs of pregnancy by losing weight gained in the previous wet season. It may be energetically more efficient in the long run to do without some food if the cost per unit of food is high, as in the dry season.

Since the dry season is the limiting period, a female's nutrient or fat level at the beginning of that season would determine whether she reproduced. That determination would be made during a window of opportunity defined by environmental cues, perhaps chemical cues in the animals' diet due to a change in the diet or an alteration of the chemical makeup of plants in their diet. Certain compounds (estrogens, toxins or others) may become concentrated during periods of stress for plants.

The lack of synchrony among females reproducing may be partly due to two factors: 1) each female must wait for the right nutrition level (within a broad window determined by environmental factors); and 2) the irregular nature of the commencement of the wet season may make the window broader and lessen the penalty for missing the perfect date. This scenario would fit with the usual reproductive pattern of the study animals, which rarely reproduce in consecutive years, and provide an explanation for the exceptions. It also

explains why the data showed no differences between the activity patterns of reproductive and nonreproductive females. By the time the sampling started in May, the monkeys were already into the wet season, when food was no longer limiting.

### Conclusions

This study was designed to test the premise that the increased energy demands of pregnancy and lactation would be reflected in altered activity budgets of female capuchin monkeys. The data showed no significant differences between the activities of reproductive and nonreproductive females. The most likely explanation is that during the dry season, the animals may be losing weight and incurring an energy debt. Alternatively, the lack of differences in the data may be due to sampling error or small sample size. During the wet season, capuchins are not food-limited; their caloric intake is often limited only by their digestive processes. This situation is partly due to adaptive traits that fit the animals to their habitat, and partly due to the unique conditions at the study site that make it unusually benign at present for the monkeys. Reproductive females may gain less weight during the wet season than other females, due to the increased costs of supporting an infant. The observed two-year cycle among the study animals would enable reproductive animals to reproduce in one wet season, and spend the next

one building up their reserves. Under these circumstances, one would not expect to find their activity schedules different from those of other females, and the data may reflect the real situation. This scenario fits the observed reproductive pattern of capuchins, which would seem to have evolved to fit their habitat conditions. In the special case of the study population, the unusual conditions at the site may exaggerate the benefits of that adaptation.

# APPENDIX

Monthly data for individual monkeys, presented as percentages of each month's total activity

TABLE A.1. MAY DATA

| ACTIVITY<br>MONKEY         | FORAGING<br>(%) | FEEDING<br>(%) | MOVING<br>(%) | LYING<br>(%) | SITTING<br>(%) |
|----------------------------|-----------------|----------------|---------------|--------------|----------------|
| RAWDEN<br>(T=4.5)          | 32              | 4              | 38            | 10           | 16             |
| HI<br>(T=5.0)              | 32              | 8              | 34            | 11           | 11             |
| MO<br>(T=4.9)              | 22              | 6              | 44            | 14           | 13             |
| AMELIA<br>(T=5.1)          | 23              | 8              | 31            | 9            | 13             |
| WHITEY<br>(T=4.5)          | 27              | 13             | 39            | 10           | 7              |
| POINTED<br>FACE<br>(T=4.5) | 36              | 2              | 34            | 19           | 7              |
| CRAWLEY<br>(T=4.5)         | 28              | 13             | 35            | 18           | 9              |
| BECKY<br>(T=4.5)           | 14              | 7              | 26            | 13           | 21             |

TABLE A.2. JUNE DATA

| ACTIVITY<br>MONKEY         | FORAGING<br>(%) | FEEDING<br>(%) | MOVING<br>(%) | LYING<br>(%) | SITTING<br>(%) |
|----------------------------|-----------------|----------------|---------------|--------------|----------------|
| RAWDEN<br>(T=4.4)          | 32              | 17             | 45            | 0            | 5              |
| HI<br>(T=4.5)              | 29              | 25             | 36            | 06           | 4              |
| MO<br>(T=4.5)              | 25              | 33             | 26            | 12           | 4              |
| AMELIA<br>(T=5.0)          | 25              | 8              | 36            | 17           | 5              |
| WHITEY<br>(T=4.5)          | 26              | 24             | 27            | 12           | 6              |
| POINTED<br>FACE<br>(T=4.5) | 32              | 22             | 30            | 13           | 3              |
| CRAWLEY<br>(T=4.4)         | 20              | 37             | 29            | 8            | 5              |
| BECKY<br>(T=4.8)           | 13              | 20             | 33            | 15           | 10             |

TABLE A.3. JULY DATA

| ACTIVITY<br>MONKEY         | FORAGING<br>(%) | FEEDING<br>(%) | MOVING<br>(%) | LYING<br>(%) | SITTING<br>(%) |
|----------------------------|-----------------|----------------|---------------|--------------|----------------|
| RAWDEN<br>(T=3.2)          | 38              | 9              | 39            | 1            | 2              |
| HI<br>(T=4.5)              | 31              | 23             | 28            | 2            | 11             |
| MO<br>(T=3.2)              | 43              | 11             | 34            | 1            | 8              |
| AMELIA<br>(T=4.8)          | 29              | 29             | 35            | 2            | 6              |
| WHITEY<br>(T=5.2)          | 40              | 29             | 24            | 0            | 4              |
| POINTED<br>FACE<br>(T=3.6) | 71              | 5              | 18            | 0            | 5              |
| CRAWLEY<br>(T=4.3)         | 44              | 16             | 31            | 0            | 7              |
| BECKY<br>(T=4.8)           | 36              | 16             | 36            | 1            | 10             |
| PINOCCHIO<br>(T=4.5)       | 22              | 9              | 38            | 2            | 16             |

TABLE A.4. AUGUST DATA

| ACTIVITY<br>MONKEY | FORAGING<br>(%) | FEEDING<br>(%) | MOVING<br>(%) | LYING<br>(%) | SITTING<br>(%) |
|--------------------|-----------------|----------------|---------------|--------------|----------------|
| RAWDEN             | 17              | 30             | 34            | 9            | 6              |
| HI                 | 25              | 25             | 40            | 4            | 3              |
| MO                 | 24              | 31             | 24            | 11           | 8              |
| AMELIA             | 26              | 26             | 30            | 8            | 9              |
| WHITEY             | 5               | 39             | 34            | 0            | 23             |
| POINTED<br>FACE    | 14              | 41             | 30            | 4            | 10             |
| CRAWLEY            | 25              | 34             | 31            | 1            | 8              |
| BECKY              | 25              | 34             | 31            | 1            | 8              |
| PINOCCHIO          | 10              | 33             | 31            | 4            | 8              |



TABLE A.5. SEPTEMBER DATA

| ACTIVITY                   | FORAGING | FEEDING | MOVING | LYING | SITTING |
|----------------------------|----------|---------|--------|-------|---------|
| MONKEY                     | (%)      | (%)     | (%)    | (%)   | (%)     |
| RAWDEN<br>(T=3.6)          | 28       | 36      | 34     | 0     | 2       |
| HI<br>(T=4.0)              | 29       | 36      | 25     | 7     | 3       |
| MO<br>(T=4.3)              | 41       | 29      | 24     | 1     | 5       |
| AMELIA<br>(T=5.7)          | 22       | 32      | 40     | 0     | 5       |
| WHITEY<br>(T=4.2)          | 9        | 60      | 29     | -     | 2       |
| POINTED<br>FACE<br>(T=4.0) | 28       | 47      | 23     | 1     | 2       |
| CRAWLEY<br>(T=4.1)         | 41       | 27      | 22     | 4     | 5       |
| BECKY<br>(T=4.3)           | 11       | 34      | 29     | 2     | 22      |
| PINOCCHIO<br>(T=4.1)       | 4        | 37      | 55     | 2     | 1       |

TABLE A.6. OCTOBER DATA

| ACTIVITY             | FORAGING | FEEDING | MOVING | LYING | SITTING |
|----------------------|----------|---------|--------|-------|---------|
| MONKEY               | %        | (%)     | (%)    | (%)   | (%)     |
| HI<br>(T=4.1)        | 16       | 27      | 32     | 8     | 10      |
| MO<br>(T=3.2)        | 12       | 35      | 51     | -     | 2       |
| WHITEY<br>(T=2.8)    | 9        | 45      | 28     | 3     | 13      |
| CRAWLEY<br>(T=4.8)   | 15       | 44      | 30     | 0     | 11      |
| BECKY<br>(T=4.2)     | 37       | 17      | 44     | -     | 3       |
| PINOCCHIO<br>(T=7.2) | 21       | 32      | 37     | -     | 11      |

TABLE A.7. NOVEMBER DATA

| ACTIVITY                   | FORAGING | FEEDING | MOVING | LYING | SITTING |
|----------------------------|----------|---------|--------|-------|---------|
| MONKEY                     | (%)      | (%)     | (%)    | (%)   | (%)     |
| RAWDEN<br>(T=4.2)          | 36       | 29      | 32     | -     | 4       |
| HI<br>(T=5.1)              | 20       | 41      | 36     | -     | 3       |
| MO<br>(T=4.2)              | 48       | 11      | 29     | 0     | 10      |
| AMELIA<br>(T=4.0)          | 6        | 48      | 37     | 0     | 4       |
| WHITEY<br>(T=4.3)          | 19       | 31      | 29     | 4     | 15      |
| POINTED<br>FACE<br>(T=3.9) | 27       | 20      | 34     | 4     | 15      |
| CRAWLEY<br>(T=4.2)         | 11       | 41      | 33     | 0     | 14      |
| BECKY<br>(T=5.5)           | 8        | 47      | 34     | 0     | 11      |
| PINOCCHIO<br>(T=4.3)       | 29       | 25      | 31     | -     | 14      |

TABLE A.8. DECEMBER DATA

| ACTIVITY                   | FORAGING | FEEDING | MOVING | LYING | SITTING |
|----------------------------|----------|---------|--------|-------|---------|
| MONKEY                     | (%)      | (%)     | (%)    | (%)   | (%)     |
| RAWDEN<br>(T=2.0)          | 38       | 35      | 24     | 0     | 4       |
| HI<br>(T=4.8)              | 46       | 29      | 20     | -     | 5       |
| MO<br>(T=3.3)              | 40       | 34      | 20     | 1     | 6       |
| AMELIA<br>(T=4.2)          | 33       | 34      | 30     | 0     | 2       |
| WHITEY<br>(T=4.3)          | 57       | 9       | 30     | -     | 5       |
| POINTED<br>FACE<br>(T=4.0) | 30       | 37      | 26     | 1     | 6       |
| CRAWLEY<br>(T=4.0)         | 50       | 17      | 28     | -     | 4       |
| BECKY<br>(T=2.2)           | 46       | 29      | 14     | -     | 11      |
| PINOCCHIO<br>(T=3.3)       | 35       | 38      | 26     | -     | 1       |

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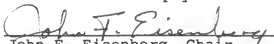
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
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